Feature

Moving in the third dimension

Every day, there is a massive movement of biomass up and down in the water column in what is likely the largest mass migration of animals on the planet. New research is shedding light on the drivers of these migrations and their significance to ecosystems and future climate change. **Cyrus Martin** reports.

The subject of animal migration typically conjures up images of great wildebeest herds moving in unison across the African continent. Or maybe flocks of Canadian geese in V-formation heading south for the winter spring to mind. There are countless examples, where, faced with surroundings that change with the seasons, instead of adapting to the environment animals have opted for the second obvious choice — moving to more favorable climes. These north–south movements across the Earth's surface aren't the end of the story, however. In addition to the XY plane, there can also be migrations along the Z axis. Paddling offshore in a kayak just before dawn puts one in close contact with just such a migration. While conditions may be tranquil at the surface as the prow of your vessel slices effortlessly through a gently undulating sea, life down below is on the move. Every day, in all the world's lakes and oceans, a multitude of creatures of all shapes and sizes move up and down in the water column in what is perhaps the largest migration of them all — diel vertical migration.

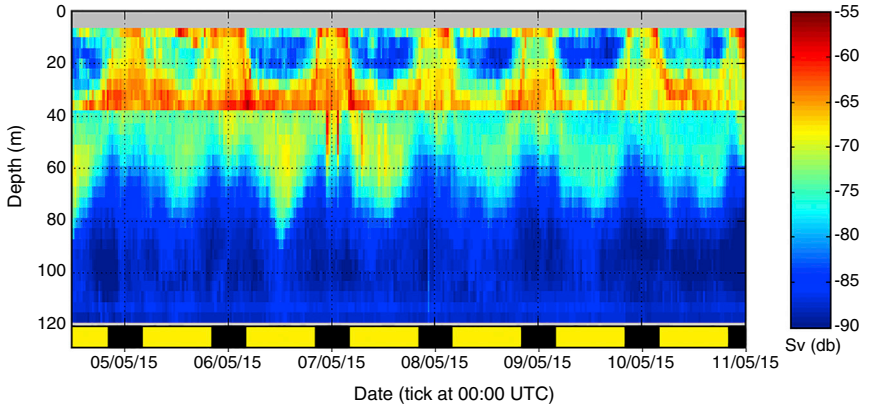
While it has been appreciated for centuries that some aquatic animals change depth in a rhythmic, daily pattern, modern research on diel (meaning 24-hour) vertical migration can be traced back to World War II, when the US navy was first using echolocation to map the sea bottom. They found some disturbing anomalies while peering through their scopes, in particular 'false bottoms' that seemed to change in depth with time of day. One interpretation of these sonar blips was that they were enemy submarines, but researchers eventually came to appreciate that what they were seeing were not Nazi U-boats but in fact large aggregates of animals called zooplankton moving between depths in regular patterns.

Small crustaceans known as copepods are a typical example. These creatures feed on single-celled algae called phytoplankton that float near the surface where there is adequate light for photosynthesis. But danger lurks nearby. Swimming to the surface willy-nilly for food puts one at risk of being made a meal of instead. Copepods are hunted by fish, which are visual predators, so it makes sense for the copepods to ascend only under cover of darkness. The adage often used to sum up this adaptive behavior is 'better off hungry than dead'. And this is how the typical pattern unfolds. Like aquatic vampires, zooplankton will rise to the surface just after dusk to feed, and then retreat to the depths below before dawn, setting up a daily mass migration that can be seen on sonar as a 24-hour oscillation.

Light and diel vertical migration

It is clear that light is a key driver of diel vertical migration. This was dramatically demonstrated last summer during the solar eclipse in North America, where researchers and students on a vessel off the Oregon coast showed that zooplankton surged to the surface when the sun became obscured by the moon, apparently 'tricking' them into thinking it was dusk. But this begs the question: what happens in environments shrouded in darkness for long periods of time, such as at those near the poles during the winter?

In a study from 2009, Berge *et al*. looked at this issue in the Arctic and found that, astonishingly, robust vertical migrations occur here too (Berge *et al*. (2009). Biol. Lett. *5*, 69–72). At a time when most life was expected to be in a dormant state, the researchers instead found that organisms moved up and down in the water column in a regular rhythm, just as occurs at other times of the year or closer to the equator. One speculation is that, while the amount of light during the polar night may be undetectable by the human eye, there are still enough stray photons penetrating the surface for zooplankton to detect them, triggering their daily movements. Of course, what this also implies is that there must be predators, fittingly called 'werewolves' by the researchers, that can visually hunt under such dim light conditions. More recently, and nicely tying into the werewolf theme, the same research team has discovered that light from the moon can also be an important stimulator of migratory behavior in zooplankton, but in this



They have rhythm: Echolocation is the modern tool of choice to study diel vertical migrations. As seen in this echogram, which records data from sonar used to detect deep scattering layers, a clear 24-hour pattern emerges. This represents the mass movement of zooplankton from the surface to deeper depths and back again. (Image courtesy of S. Häfker.)

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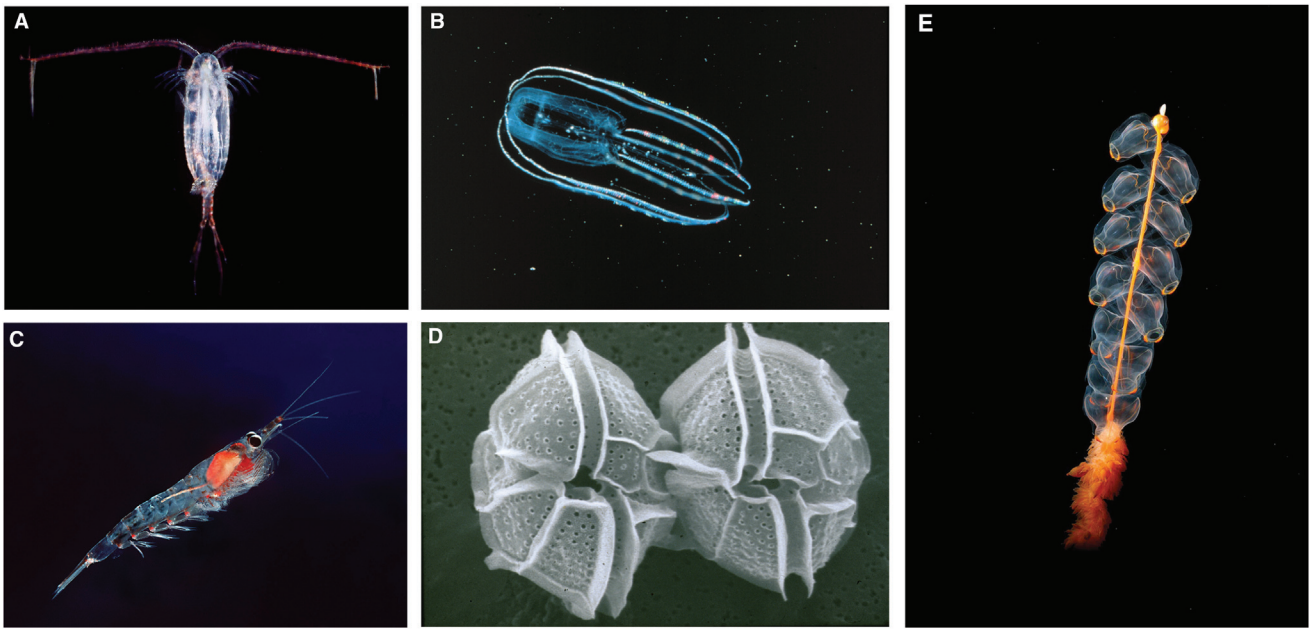


The commuters: The zooplankton moving up and down in the water column are a diverse assemblage of unicellular and multicellular creatures including (A) copepods (image from Wikimedia Commons), (B) ctenophores (image from NOAA photo gallery), (C) krill (photo by Uwe Kils), (D) dinoflagellates (image from CSIRO) and (E) siphonophores (image from Wikimedia Commons).

case the rhythms are not 24 hours but rather correlate with the lunar cycle (Last *et al*. (2016). Curr. Biol. *26*, 244–251). By overlaying their sonar data with the lunar cycle, they could clearly show the stimulatory effect of moonlight, which became pronounced during the full moon, when the zooplankton were seen to plunge in unison to the depths, presumably eluding the werewolves patrolling the surface.

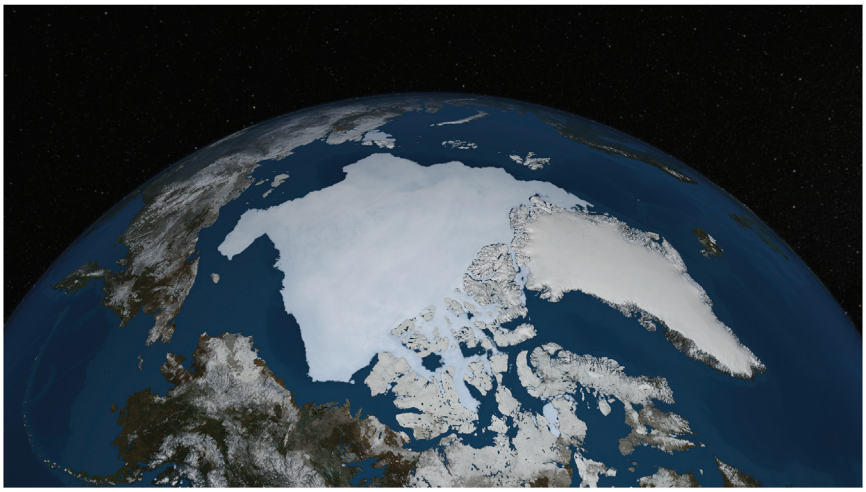
As research on diel vertical migrations progresses, the story becomes even more complex, both in terms of the behaviors themselves and the stimuli. In some cases, like drunks driving the wrong way up a freeway exit ramp, migrants will move against the normal flow of traffic, swimming to the surface during the day, and down below at night. The significance of this asynchronous behavior is unclear, but may be an adaptation to avoid predators moving in the standard diel vertical migration pattern.

And a model of diel vertical migration driven by light alone is far too simplistic. This migration can be triggered by other cues, such as the predators themselves. It has been observed in both freshwater and marine studies, for example, that the removal of predators causes the rhythmic migrations to weaken or cease entirely. Presumably, the zooplankton can sense the presence of predators directly, perhaps by detecting kairomones — chemicals specifically exuded by predators. In this way, zooplankton can flexibly engage in light-dependent migratory behavior, and this is presumably an adaptation to avoid wasting energy when predators aren't stalking them.

The role of internal clocks

Light and other external factors have a strong, direct influence on diel vertical migration, but it is now appreciated that internal biological clocks also control rhythms in physiology and behavior in all domains of life, from bacteria to plants and animals. Their importance is underlined by the 2018 Nobel Prize in Physiology and Medicine, which was awarded for research on circadian clocks. The key attribute of a circadian (from 'circa' meaning 'about', and 'diem' meaning day) rhythm is an oscillation of about 24 hours that persists in the absence of any external influences. Work in a number of organisms has dissected in exquisite detail how, at the molecular level, such a rhythm can be produced. But, molecular mechanisms aside, the real utility of a circadian clock is that it endows an organism with the ability to 'anticipate' and prepare for future conditions rather than reacting to them as they arise. The advantage of such an internal timing device is clear considering that circadian clocks have evolved everywhere we look. In the case of zooplankton migrating in the water column, it would make much more sense to start migrating downward to safety before first light, rather than waiting for the sunrise when it might be too late to avoid being devoured.

Although circadian clocks appear to be ubiquitous, most of the research has been in done in model organisms, so there is currently very little known about the role of circadian clocks in zooplankton, which are difficult to study in the laboratory. However, a few studies have begun to trickle in. Recently, Häfker and colleagues showed that the migratory behavior of copepods is, at least in part, driven by a circadian clock (Häfker *et al*. (2017) Curr. Biol. *27*, 2194–2201). By bringing the animals into the laboratory and putting them in small, acrylic columns under constant darkness, Häfker *et al*. observed that the tiny creatures exhibited



Melting the top off of diel vertical migration: As the ice caps diminish with global warming, it is expected that this will stimulate diel vertical migrations, with potentially important consequences for the sequestration of carbon. (Image from Wikimedia Commons.)

diel vertical migration with a period of approximately 24 hours. At the physiological level, the researchers also saw that respiration was under circadian control, and that animals under normal light–dark conditions showed a burst of metabolism just before they swam upwards. This early burst may help the animal prepare for its arduous journey to the surface. The scale of these animals makes swimming in water as difficult as a person doing a crawl stroke in a pool filled with honey, so they need all the help they can get. And it is this anticipatory, preparatory nature of the circadian clock that may help make this possible.

Putting all of this together, the picture that emerges is one in which the causes of diel vertical migration are many. The ultimate cause appears to be the presence of visually guided predators, but the proximate causes seem to be a combination of external environmental cues and internal timing mechanisms to produce a behavior that is optimally suited to avoid predators.

Diel vertical migration and climate change

As impressive as diel vertical migration is in its own right, the behavior is also the subject of intense investigation because of its importance to ecosystems, and in particular geochemical cycles. Much of the recent activity has focused on the role of diel vertical migration in the 'biological pump', a natural process that removes carbon from the air and sequesters it in the depths of the ocean. In a simplified version or this process, carbon is absorbed from the air near the surface by phytoplankton, which are then consumed by organisms farther up the food chain. These animals then defecate, and their fecal pellets float down to the bottom where they are effectively locked away. Alternatively, any carbon absorbed by the animal may find its way to the bottom when the animal dies and its corpse sinks. But if diel vertical migration is added to the mix, it can supercharge the pump. Copepods, for example, will feed at the surface at night and then, as we've seen, swim down to depth during the day. When they then defecate, respire, or die, the movement of carbon downwards is greatly accelerated compared with when the effect of this migration is excluded.

Given the importance of diel vertical migration to the movement of carbon, there is interest in the relationship between migration and climate change. As can be seen from the work in the Arctic, although zooplankton still exhibit migration in low light, stronger light–dark cycles are expected to enhance migratory behavior. So with the loss of sea ice at the poles in the future, we can expect more robust diel vertical migration, which may help sequester more carbon through the biological pump. One important caveat, however, is that the effect of enhanced diel vertical migration may be overshadowed by other components of the biological pump. For example, algal blooms stimulated by loss of sea ice may simply aggregate and sink below in a passive process that doesn't require migrating zooplankton. Whatever the balance between passive and active mechanisms, scientists have been exploring ways to harness the biological pump as a way to mitigate carbon dioxide emissions. The idea is to artificially fertilize patches of the ocean with nutrients like iron, which stimulates phytoplankton growth. A better understanding of diel vertical migration — and other components of the pump — will help determine the feasibility of such efforts.

Unraveling the mysteries of the sea

There are many questions left to address about the mysterious daily undulations of life under the sea. These questions are related to more general questions being asked by ocean scientists. We are still at a very early stage in characterizing life in the oceans, especially single-celled life. Some recent sampling efforts, such as the TARA Oceans project, suggest there is a vast hidden trove of biological diversity in the oceans waiting to be discovered. Once we know who is there, the even harder work of actually studying their biology begins. Like the case of the copepods, scientists would ideally like to leverage genetics to study behaviors like diel vertical migration. The emergence of new genetic tools like CRISPR will hopefully soon make this possible. And of course, we will want to know more about their life history, who they eat, and where they go. Such information will be required to better understand marine ecology in general and how important chemical processes like the biological pump work. Answering these questions will require another kind of migration, in particular a mass movement of young scientists into the marine sciences.

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